

Evolution and Biodiversity: the evolutionary basis of biodiversity and its potential for adaptation to global change

Biodiversity has a key role in maintaining healthy ecosystems and thereby sustaining ecosystem services to the ever-growing human population. To get an idea of the range of ecosystem services that we use daily, think of how much energy and time it would cost to make Mars (or some other Earth-like planet) hospitable for human life, for example, in terms of atmosphere regulation, freshwater production, soil formation, nutrient cycles, regulation of climate, etc. On our own planet, that process took four billion years and required the contribution of a vast amount of functions performed by different life forms, ultimately driven by evolution and that is only the top of the (melting) iceberg.

Unfortunately, the ecosystems that we so exploit and dearly need for our long-term survival and welfare are jeopardized by our own actions. Global change, triggered by human activities, is all around us. The pervasive effects of climate change, habitat loss and fragmentation, over-harvesting, pollution, altered nutrient cycling, invasive species and interactions thereof affect virtually all Earth's ecosystems (Rockström et al. 2009). With seven billion people consuming natural resources more rapidly than they are created, we are at the onset of a major environmental revolution. As a consequence, species are already shifting, expanding, disappearing, changing their behaviour and phenology, exploiting newly available food resources and abandoning scarcer ones. Ecosystems are changing too, driven by changes in environmental drivers and by the reshuffling of their biota into previously unknown combinations of species (Williams and Jackson 2007). The interplay of all these processes makes the forecast of changes in ecosystem services a daunting task.

All these changes are likely to have a bearing on and be influenced by the evolutionary forces at play. The main legacy of Charles Darwin was to make us realize that we owe everything, including the formation of our own species, to evolution. We thus learned that the history of life is driven by evolution. But what about the future? What is the contribution of evolution to these ecological changes? And, probably most relevant to policy: what is the potential of evolutionary processes to exacerbate or mitigate the effects of global change? Is evolutionary biology just a scientific gimmick compared to the real problems that we are facing? This volume deals exactly with these questions.

Until a decade or so ago, evolutionary change was broadly assumed to happen on a vastly longer time scale than ecological change. As a corollary, our view on biodiversity and ecosystem functioning has often been static, trying to conserve biodiversity as it is, and preferably, as it once was. Just like our ecosystems, however, this paradigm is shifting. The closer we look at adaptive evolution, often with the aid of new biological insights and technological advances, the faster it seems to happen. Evolution and ecology are proving to be so heavily entwined that the distinction is becoming increasingly hard to make. This knowledge profoundly affects our thinking on how evolution affects patterns of biodiversity, especially in the face of global change. Adaptive responses to climate change, for example, have been shown to occur within a single generation (Van Doorslaer et al. 2007). Contemporary evolution is probably more important than we assumed to date and is, therefore, likely to mediate the response of populations, species, communities and ecosystems to both gradual and sudden environmental change.

In April 2010, the European Platform for Biodiversity Research Strategy (<http://www.epbrs.org>) hosted the meeting 'Evolution and Biodiversity: The evolutionary basis of biodiversity and its potential for adaptation to global change', funded by the BioStrat project (<http://www.biostrat.org>). The meeting was preceded by an electronic conference that lasted 21 days and gathered over 62 contributors and more than 1600 participants (Grant et al. 2010). Both the conference and the meeting revolved around three main themes: (i) the evolutionary basis of biodiversity, (ii) evolutionary responses to global change and (iii) evolution in complex systems and co-evolutionary networks. This special issue builds from the diverse arrangement of contributions made at the conference and aims to provide a diverse and interdisciplinary perspective on the interplay between evolutionary and ecological responses in the face of global change.

Content of the special issue

For those still in doubt on the ubiquitous nature of contemporary evolution, Shine (2012) opens this special issue with a review on evolutionary aspects of biological invasions, focussing on both the invading species as the invaded ecosystems. By showing how evolution can

rapidly modify ecologically relevant traits in invading as well as native species, his paper exemplifies the dynamic nature of contemporary evolution as a response to strong selection.

For genetic evolution to occur, genetic diversity for ecologically relevant traits is a necessary precondition. The paradox for many species, however, is that they need to adapt fast to a plethora of stressors related to global change while suffering population declines as a consequence of global change itself. Because population declines enhance genetic erosion and drift and constrain adaptive evolution, the conditions for adaptation deteriorate further. To make things worse, inbreeding depression in small populations further reduces fitness. Bijlsma and Loeschcke (2012) tackle the interaction of drift, inbreeding and environmental stress and its negative consequences for rapid adaptation. They review empirical evidence for several mechanisms underpinning this unfortunate synergy, but also call for more research aimed at dissecting its causation and consequences. A most promising avenue for such mechanistic research on the basis of inbreeding depression lies in the field of conservation genomics. Angeloni et al. (2012) provide a conceptual toolbox for genomic research in conservation biology and highlight some of its possibilities for the mechanistic study of functional variation, adaptation and inbreeding.

Van Dyck (2012) takes on the discrepancy of how an organism perceives its environment and how we, humans, typically represent it. For the sake of simplicity, the habitat of each species is often regarded as a static entity in space and time and assimilated to a single vegetation or landscape type. The European Habitats Directive, the cornerstone of Europe's nature conservation policy, exemplifies this view (Council Directive 92/43/EEC). Van Dyck argues that applied species conservation could benefit greatly from the application of an eco-evolutionary framework and illustrates his argument richly with both theoretical and applied examples. He also shows that an organism's perception of its environment is subject to selection, a mechanism that could reduce the initial impact of environmental degradation or alleviate it over the longer run.

Urban et al. (2012) focus on the necessity to include evolutionary processes in community ecology and fully sever from the classical view of different temporal scales for ecology and evolution. They argue that certain consequences of global change can only be accounted for by interactions between ecological and evolutionary processes. Their paper is rooted in the conceptual framework of eco-evolutionary dynamics, which integrates diversity within and among species (populations and communities) across multiple spatial scales in heterogeneous landscapes and which includes the role of dispersal in mediating

both species sorting and local adaptation. By including evolutionary dynamics into metacommunity models, they aim to increase the accuracy and realism of simulated effects of global change on biodiversity patterns.

Lemaire et al. (2012) provide an empirical study on the genetic interaction between toxic cyanobacteria and the waterfleas that graze on them. This study, which builds on the concepts of the geographic mosaic of coevolution (Thompson 2005) and of eco-evolutionary dynamics (Fussmann et al. 2007), highlights the important role of evolution in predator–prey interactions – a process that is typically viewed as ecological. Their experiments represent a promising basis for future control of toxic cyanobacteria blooms, a particularly important application in a world that faces increasing demands of clean freshwater.

Focussing further on eco-evolutionary interactions, Palkovacs et al. (2012) review studies on phenotypic change in response to human activities. They show that phenotypic change can sometimes cascade across populations, communities and even entire ecosystems; however, it can also show the opposite trend – counteracting the effect of environmental change on traits. In the former case, evolution amplifies the initial change; in the latter, it mitigates its effects. Identifying the mechanisms behind both types of outcomes is essential to predict and manage the effects of global change.

Phenotypic change in response to external drivers can have various causes. Typically, we associate it with either plasticity (nonheritable) or genetic (heritable) evolution. Bonduriansky et al. (2012) target the interface between both, looking at nongenetic inheritance and its role in adaptation. They dissect the diversity of epigenetic and other transgenerational effects, and their role in adaptation and maladaptation. Because very little is still known about the role played by this kind of inheritance in evolutionary processes, they also present a research framework for future studies.

Finally, Santamaria and Méndez (2012) build on the information reviewed in all previous papers to identify recent advances in evolutionary knowledge of particular importance to improve or complement current biodiversity policy. They follow by examining their incorporation (or lack thereof) into international biodiversity policy and identifying avenues for innovation and improvement – focusing on the Convention on Biological Diversity and the European biodiversity policy. Their review shows numerous opportunities for the integration of evolutionary knowledge into several sectoral policies of direct relevance for biodiversity – including nature conservation, fisheries, agriculture, water resources, spatial planning and climate change. They, however, conclude with a humbling remark: these avenues for improvement are challenged by the low level of enforcement of biodiversity policies

(largely owing to their nonbinding nature) and the decreasing importance given to biodiversity research.

Overall, these nine papers offer compelling evidence for the role of evolutionary processes in the maintenance of biodiversity and the adaptation to global change. How should we proceed from here? Immediate priorities probably include work to improve the integration of evolutionary framework into other fields of biology (see also Carroll *et al.* 2010), to apply this knowledge into conservation practice and, most importantly, to translate this knowledge to policy makers and natural-resource managers. We have never been more knowledgeable on eco-evolutionary mechanisms, causations and interactions – both across space and time, and in realistic settings; yet it must be clear that, despite the availability of more and better information, accurately predicting future changes in evolving ecosystems makes as little sense as predicting next year's weather day by day. Contingency is an inherent component of life; hence, modelling with better parameter estimates and more complex algorithms will not necessarily make us better fortune-tellers (Boero *et al.* 2004). In their search for funding, recognition and/or governance panaceas (*sensu* Ostrom *et al.* 2007), scientists, managers and policy makers easily lose sight of this unpopular, but irrefutable, fact. Evolutionary biology is a probabilistic science fraught with uncertainties, but these uncertainties don't make evolutionary insights less valuable. Translating them into practice represents an unavoidable challenge – in which we are aided, fortunately, by the development of methodologies that incorporate complexity and uncertainty into the making and implementation of policies (e.g. adaptive management, ecosystem management, transition management; Christensen *et al.* 1996; Brugge and Raak 2007; Brock and Carpenter 2007).

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Literature cited

- Angeloni, F., C. A. M. Wagemaker, P. Vergeer, and N. J. Ouborg. 2012. Genomic toolboxes for conservation biologists. *Evolutionary Applications* 5:130–143.
- Bijlsma, R., and V. Loeschcke. 2012. Genetic erosion impedes adaptive responses to stressful environments. *Evolutionary Applications* 5:117–129.
- Boero, F., G. Belmonte, S. Bussotti, G. Fanelli, S. Fraschetti, A. Giangrande, C. Gravili *et al.* 2004. From biodiversity and ecosystem functioning to the roots of ecological complexity. *Ecological Complexity* 2:101–109.
- Bonduriansky, R., A. J. Crean, and D. T. Day. 2012. The implications of nongenetic inheritance for evolution in changing environments. *Evolutionary Applications* 5:192–201.
- Brock, W. A., and S. R. Carpenter. 2007. Panaceas and diversification of environmental policy. *Proceedings of the National Academy of Sciences of the United States of America* 104:15206–15211. doi: 10.1073/pnas.0702096104.
- Brugge, R. V. D., and R. V. Raak. 2007. Facing the adaptive management challenge: insights from transition management. *Ecology and Society* 12:33.
- Carroll, S., M. T. Kinnison, and L. Bernatchez. 2010. In light of evolution: interdisciplinary challenges in food, health, and the environment. *Evolutionary Applications* 4:155–158.
- Christensen, N. L., A. M. Bartuska, J. H. Brown, S. Carpenter, C. D'Antonio, R. Francis, J. F. Franklin *et al.* 1996. The Report of the Ecological Society of America Committee on the Scientific Basis for Ecosystem Management. *Ecological Applications* 6:665–691.
- Fussmann, G. F., M. Loreau, and P. A. Abrams. 2007. Eco-evolutionary dynamics of communities and ecosystems. *Functional Ecology* 21:465–477.
- Grant, F., J. Mergeay, L. Santamaria, J. Young, and A. D. Watt. 2010. Evolution and biodiversity: the evolutionary basis of biodiversity and its potential for adaptation to global change. Conference report 1–19 March 2010. Retrieved from http://www.epbrs.org/PDF/Evolution and Biodiversity_longversion_final.pdf.
- Lemaire, V., S. Bruscotti, I. Van Gremberghe, W. Vyverman, J. Vano-verbeke, and L. De Meester. 2012. Genotype x genotype interactions between the toxic cyanobacterium *Microcystis* and its grazer, the water flea *Daphnia*. *Evolutionary Applications* 5:168–182.
- Ostrom, E., M. A. Janssen, and J. M. Anderies. 2007. Going beyond panaceas. *Proceedings of the National Academy of Sciences of the United States of America* 104:15176–15178. doi: 10.1073/pnas.0701886104.
- Palkovacs, E., M. T. Kinnison, C. Correa, C. M. Dalton, and A. Hendry. 2012. Ecological consequences of human-induced trait change: fates beyond traits. *Evolutionary Applications* 5:183–191.
- Rockström, J., W. Steffen, K. Noone, Å. Persson, F. S. I. Chapin, E. F. Lambin, T. M. Lenton *et al.* 2009. A safe operating space for humanity. *Nature* 461:472–475.

- Santamaría, L., and P. F. Méndez. 2012. Evolution in biodiversity policy - current gaps and future needs. *Evolutionary Applications* 5:202–218.
- Shine, R.. 2012. Invasive species as drivers of evolutionary change: cane toads in tropical Australia. *Evolutionary Applications* 5:107–116.
- Thompson, J. N. 2005. *The Geographic Mosaic of Coevolution*. University of Chicago Press, Chicago, USA.
- Urban, M. C., L. De Meester, M. Vellend, R. Stoks, and J. Vano-
verbeke. 2012. A crucial step towards realism: responses to climate change from an evolving metacommunity perspective. *Evolutionary Applications* 5:154–167.
- Van Doorslaer, W., R. Stoks, E. Jeppesen, and L. De Meester. 2007. Adaptive microevolutionary responses to simulated global warming in *Simocephalus vetulus*: a mesocosm study. *Global Change Biology* 13:878–886.
- Van Dyck, H. 2012. Changing organisms in rapidly changing anthropogenic landscapes: the significance of the “Umwelt”-concept and functional habitat for animal conservation. *Evolutionary Applications* 5:144–153.
- Williams, J. W., and S. T. Jackson. 2007. Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment* 5:475–482.